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WESTERN ATLANTIC SPECIES OF THE PARASITIC GENUS *LEIDYA* (EPICARIDEA: BOPYRIDAE)

By Roland Bourdon and Thomas E. Bowman
Station Biologique, Roscoff and Smithsonian Institution Washington, D. C.

The first species of *Leidya* was discovered on the fiddler crab *Uca pugilator* (Bosc) in New Jersey by Leidy (1855), who described it briefly under the name *Cepon distortus*. The differences between Leidy's species and the only other species of *Cepon* then known, *C. typus* Duvernoy from Mauritius, were great enough to lead Cornalia and Panceri (1858) to establish the genus *Leidya* for the American parasite. Richardson (1908) described as *Leidya distorta* specimens collected the same year by Verrill from the shore crab, *Pachygrapsus transversus* (Gibbes), in Bermuda. Other specimens of *Leidya* were reported by A. S. Pearse from *Uca pugilator* at Beaufort, North Carolina (Pearse, 1947), and from *Pachygrapsus transversus* at Bimini, Bahamas (Pearse, 1951). Pearse was obviously unaware of Richardson's (1908) Bermuda record and established a second species, *Leidya bimini*, for the parasites of *Pachygrapsus*. The diagnosis of *L. bimini* is very short and only the male was illustrated in toto. The characters that Pearse used to separate the 2 species are of little value and are also rather variable among individuals. In fact, the only one of Pearse's criteria that is not found in descriptions of *L. distorta* is the presence of medioventral tubercles on the male of *L. bimini*, not mentioned in the descriptions of *L. distorta* by Leidy and by Richardson, altho we have found them to be present in the later species.

The discovery of a pair of *L. bimini* on *Cyclograpsus integer*

(H. Milne-Edwards) at Jamaica by Hartnoll (1965) provided us the opportunity of examining the question of whether the 2 species are really distinct, a question that had remained unresolved because of the difficulty in obtaining specimens of *Leidya*. In the meantime, one of us (R. B.) received from Dr. L. B. Holthuis (Rijksmuseum van Natuurlijke Historie, Leiden) a specimen of *Uca vocator* (Herbst) from Trinidad collected by Dr. Von Hagen, parasitized by 2 pairs of bopyrids. Examination of these bopyrids raised a new problem. Altho the males with their characteristic long slender uropods unquestionably belonged to the genus *Leidya*, the presence of endopods on the pleopods of the females complicated matters, since the diagnosis of *Leidya* distinguished it from other genera of the *Cepon* group (except *Mesocepon*) by its lack of pleopodal endopods. However, as will be shown herein the pleopods of both *L. distorta* and *L. bimini* possess endopods, altho they are greatly reduced in the latter species.

Mr. Richard Heard, Jr. (Marine Institute, University of Georgia), learning of our interest in the genus *Leidya*, generously sent the junior author well preserved specimens that he had collected in North Carolina and Georgia from *Pachygrapsus transversus*, *Uca pugilator*, and 2 new hosts, *Uca minax* (Le Conte) and *Uca pugnax* (Smith). After study, these specimens were sent to the senior author, together with other specimens of *Leidya* in the collections of the Smithsonian Institution.

These collections of *Leidya*, comprising much more numerous and better preserved specimens than had been available to earlier authors have made it possible for us to describe and illustrate the 2 Western Atlantic species in greater detail than in previous accounts, to confirm their specific distinctiveness, and to point out the criteria by which they may be identified.

Leidya distorta (Leidy)

Figures 1–5

Cepon distortus Leidy, 1855, p. 150, pl. 10, fig. 26–32.—Harger, Verrill, and Smith, 1874, p. 573.—Harger, 1879, p. 157; 1881, p. 311.—Kossman, 1880, p. 122; 1881, p. 182.—Richardson, 1900, p. 309.

Leidya distorta (Leidy).—Cornalia and Panceri, 1861, p. 114.—Giard and Bonnier, 1887, p. 68, fig. 12.—Bonnier, 1900, pp. 255–257, fig.

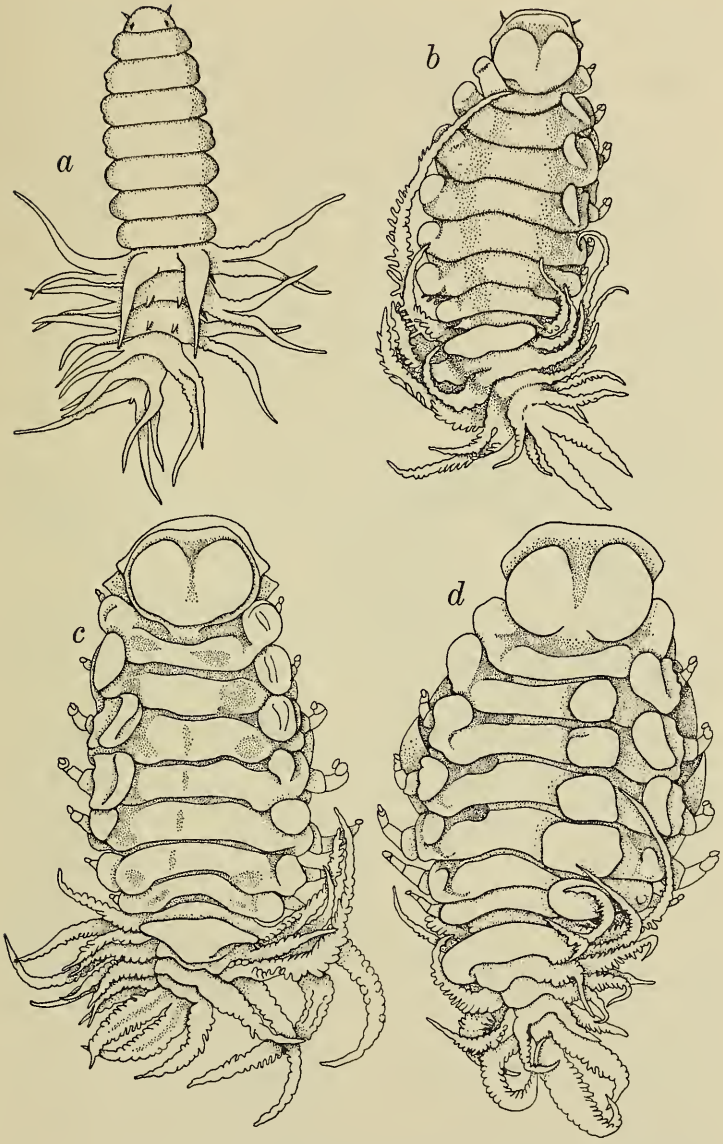

FIG. 1. *Leidya distorta* from *Uca pugilator*, females: a-b, juveniles; c, preadult; d, adult.


a
e
g
b
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f

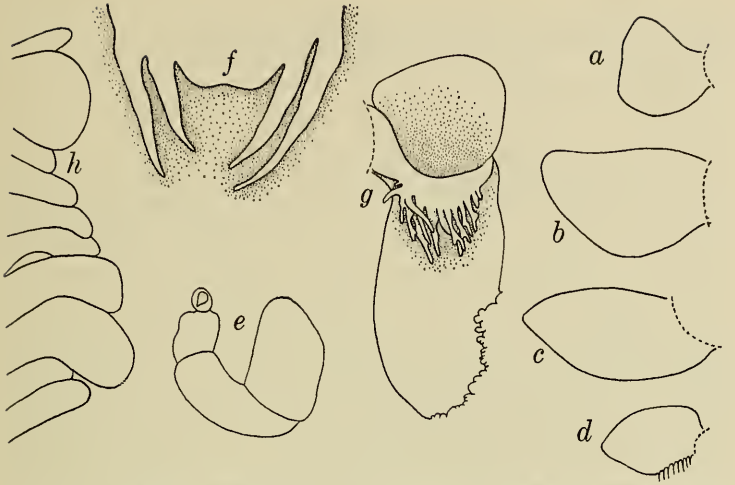

Fig. 3. *Leidya distorta* from *Uca pugilator*, adult female: a-d, oostegites 2–5; e, pereopod; f, posterior margin of head; g, 1st oostegite; h, dorsal thoracic bosses in profile.

45a-g.—Richardson, 1901, p. 579; 1904, pp. 74–75; 1905, pp. 511–512, fig. 559a-c, 560 a-d.—Pearse, 1947, p. 326.

Phryxus distortus (Leidy).—Walz, 1882, p. 183 (59).

nec *Leidya distorta* (Leidy).—Richardson, 1908, pp. 23–26, fig. 1–5 [= *Leidya bimini* Pearse].

Material examined: From *Uca pugilator* (Bosc): 2♀♀, Beaufort, North Carolina, 29 May 1946, A. S. Pearse, coll. (USNM 84046).—7♀♀, 1♂, same locality—collector, 10 July 1946 (USNM 84048).—5♀♀, 2♂♂, same locality, March 1963, R. Heard, coll. (USNM 128473).

From *Uca pugnax* (Smith): 3♀♀, Savannah, Georgia, March 1963, R. Heard, coll. (USNM 128472)

From *Uca minax* (Le Conte): 1♀, Savannah, Georgia, 15 March 1963, R. Heard, coll. (USNM 128470).

From *Uca* sp.: 1♀, Sapelo Island, Georgia, July 1961, R. Heard, coll. (USNM 128471). 1♀, Port-de-France, Guadeloupe, R. Bourdon collection.

From *Uca vocator* (Herbst): 2♀♀, 2♂♂, El Sodorro, Trinidad, Dr. Von Hagen, coll. (Rijksmuseum van Natuurlijke Historie, Leiden).

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Fig. 2. *Leidya distorta* from *Uca pugilator*, females: a, ovigerous adult; b-g, juvenile; b, 1st antenna; c, pleonites 1–3, dorsal; d, maxilliped; e, 1st oostegite; f, pleon, ventral; g, posterior margin of head; h, preadult, maxilliped and posterior margin of head.

Description: The specimens are described below in the order of their maturity, judged from the development of the oostegites.

1. From *Uca pugilator*

Female:

1. Oostegites rudimentary (Fig. 1, a)

Length 4.8 mm. Dorsal surface of anterior half of body resembling that of male: Head not at all immersed in pereon; 2nd antennae visible in dorsal view; pereon narrow, with nearly parallel margins, differing from that of the male only in that pereonites 1–4 are laterally excavated and slightly inflated at the positions of the future pleural bosses. Vestiges of ocular pigment visible at posterior angles of head. Segments 1–2 of 1st antenna (Fig. 2b) with anterolateral apophysis bearing a few setae; segment 3 minute and unarmed. Second antenna 7-segmented. Maxillipeds represented by 2 triangular lamellae with 2–3 apical setae, not reaching the base of the oral cone. Oostegites rudimentary, scarcely larger than basipods of pereopods, which increase in size posteriorly. Pleon nearly as long as pereon, with 5 pairs of long slender lateral plates with slightly tuberculate margins. Pleopods similar to epimeral plates, all biramous, endopods very short, smaller on one side than on the other. 6th pleonite ending in an anal tube, bearing a pair of uropods one-fourth longer than exopods of 5th pleopods. Dorsal surface of 1st pleonite bearing 2 foliaceous pointed processes extending back to 4th pleonite; dorsal surface of 2nd and 3rd pleonites each with a pair of small short pointed processes. To our knowledge, such processes have not been reported previously in the Bopyridae.

2. Oostegites nearly meeting medially (Fig. 1b)

Length 4.6 and 5.2 mm. General aspect as in fig. 1b. Cephalogaster and frontal lamina already developed. Eyes completely lost. Maxillipeds elongate, with marginal setae, completely covering buccal cone. Lateral margins of pereonites elevated above central part of pereon. Oostegites cordate, 1st pair divided into 2 nearly equal parts. Pereopods 5–7 much larger than pereopods 1–4. Pleonites 1–3 each with 2 small lateral digitations, all filiform in one specimen, some blunt in the other (Fig. 2c). Epimeral plates and pleopods digitate. Pleopods with endopods smooth and distinctly shorter than exopods, although relatively more developed in anterior pairs; exopod of 1st pleopod of convex side longer than that of concave side, reaching anterior to 3rd pereonite in one specimen and to posterior margin of head in other. Anterior 4 pleopods of convex side of latter specimen each with blunt lobe between endopod and exopod. Uropods slightly broader than other pleonal appendages.

3. Oostegites slightly overlapping

Length 5.2 and 5.8 mm. Maxillipeds (Fig. 2d) similar to those of preceding stage. Pleural bosses very distinct on pereonites 1–6. First oostegite

(Fig. 2e) with lobulate posterior margin on transverse inner ridge and setae on outer margin of posterior lobe. Endopods of right pleopods (Fig. 2f) longer and with more digitation than those of left pleopods. Second pleonite more enlarged than other pleonites, with well defined lateral margins. Lateral digitations of pleon completely lost in one specimen, still visible on 1st pleonite of other specimen (Fig. 1b), which despite this juvenile character, has an absolutely identically developed marsupium and is in other respects more mature; e.g. posterior margin of head has a pair of short cephalic plates (Fig. 2g).

4. Oostegites forming a completely closed marsupium.

a. Female preadult (Fig. 1c)

Length 6.1 mm. Internal cephalic plates present, as tubercles; external cephalic plates more developed. Palp of maxilliped reduced, with setae on medial margin only (Fig. 2h). Pereonites 1–6 swollen on one side near pleural bosses. Posterior lobe of 1st oostegite elongate, reaching between pereopods 3 and 4; transverse ridge with about 10 long digitations.

b. Female adult (Fig. 1d)

Length 6.4 mm. The slight dorsal inflations of the pereon that were becoming evident at the approach of maturity have developed into conspicuous subquadrangular dorsal bosses, together forming a strong carina. Marsupium convex; oostegites varying in shape according to their position (Fig. 3, a-d); 5th pair only with fringed and tuberculate outer surface. Pereopods (Fig. 3e) increase in size posteriorly as in preceding stages, but differences in size are greater; 1st pereopods appear minute in comparison with 5th and 6th pereopods.

c. Older adult female (Fig. 2a)

Length up to 7.7 mm. As size of female increases, body becomes more and more globular, dorsal bosses more voluminous, lobes on posterior margin of head (Fig. 3f) and posterior lobe of 1st oostegite (Fig. 3g) more elongate; digitations of transverse ridge of 1st oostegite tend to develop branches.

Variation: Variations in the following characters have been observed in adult females:

—Cephalogaster sometimes very prominent.

—Internal cephalic plates may be as long as external cephalic plates; the latter may reach or even extend across the midline of the body. In one specimen the inner plate had 2 small secondary filiform digitations.

—1st oostegite may extend posteriad only to the level of the 3rd pereopods or as far as the level of the 5th pereopods.

—Dorsal bosses (Fig. 3h) of the pereon vary in number from 4 to 6, and vary in prominence. In the specimen illustrated in fig. 2a the

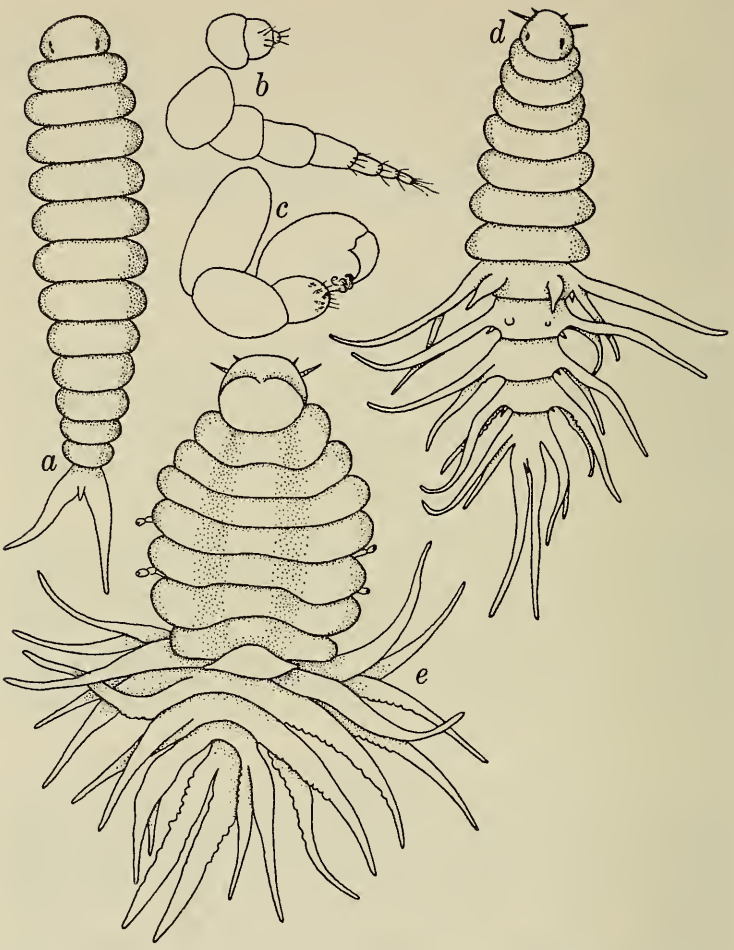

Fig. 4. *Leidya distorta*: a-c, male from *Uca pugilator*; a, habitus, dorsal; b, 1st and 2nd antennae; c, pereopod; d, juvenile female from *Uca pugnax*; e, juvenile female from *Uca minax*.

bosses form a median carina, but in all other specimens the carina is displaced to one side.

—The exopod of the longer 1st pleopods may reach anteriorly only to the 5th pereonite or as far as the posterior margin of the head.

—The large blunt lobes at the base of the rami may be present

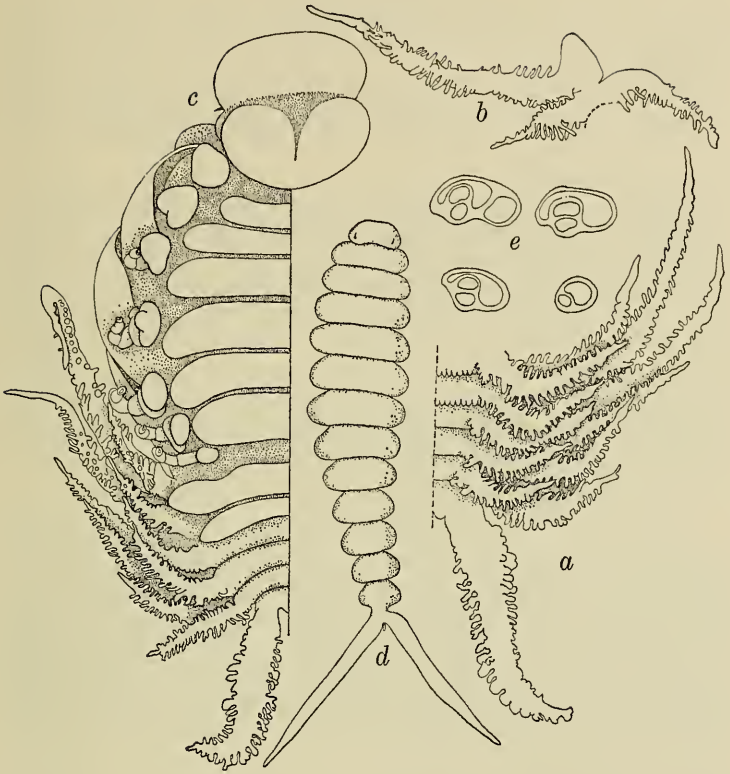

FIG. 5. *Leidya distorta* from *Uca vocator*; a-c, female; a, pleon, ventral; b, pleopod and epimeral plate of 1st pleonite; c, habitus, dorsal; d-e, male; d, habitus, dorsal; e, chitinous network of pleopods.

simultaneously on both right and left 1st and 2nd pleopods. In one specimen such a lobe was present on the 5th pleopod.

—Endopods are always present and well developed on the pleopods, more slender and from a third to a half as long as the exopod.

Male: (Figure 4a)

Length 1.8–2.7 mm. Head distinctly narrower and separate from 1st pereonite. Eyes present. First antenna 3-segmented; 2nd antenna 7-segmented (Fig. 4b). Maxilliped not observed. Pereopods (Fig. 4c) subequal, with scales on posterior margins of carpus and propodus. Pereonites

1–7 and pleonites 1–2 each with medioventral tubercle. Pleon 6-segmented. Pleopods tubercular, with a peculiar chitinous network (Fig. 5e) illustrated by Leidy (1855). Uropods long, filiform, with anal tube jutting out prominently at base.

Variation: The 2nd antenna may consist of from 5 to 8 segments. The medioventral tubercles may be present as far back as pleonite 4.

2. From *Uca pugnax*

Specimens collected from this host are all juveniles, 2 with rudimentary oostegites, the other with oostegites nearly meeting medially. Compared to parasites of similar maturity from *Uca pugilator*, the most mature female (7.1 mm) agrees closely with the description given above, and the others differ but little. The youngest (Fig. 4d), which measures 5.0 mm, has a narrower body, more slender pleonal appendages, reduced dorsal processes on pleonite 1, and those of pleonite 2 represented by blunt knobs. In the 3rd specimen (4.8 mm), in which the maxillipeds and the oostegites are slightly more developed, the pleon is enlarged and its appendages are very tuberculate and curved.

3. From *Uca minax* (Fig. 4e)

The elongate form of the maxillipeds, the degree of development of the oostegites, and regular increase in length of the pereopods indicate that this specimen is a very young female. Despite these characters, however, and the small size of the parasite (4.6 mm), it agrees in general appearance with the second specimen from *Uca pugilator* (oostegites nearly meeting medially) in having a relatively broad body, a cephalogaster and frontal plate already developed (the latter especially important), and elevated lateral margins on the pereonites.

4. From *Uca* spp.

The specimen from Guadeloupe is at the same stage of development as the specimen from *Uca minax* and in body form resembles Fig. 4e. However the pleural bosses are already present and the appendages of the pleon have many digitations on their borders. The specimen from Sapelo Island is an adult female.

5. From *Uca vocator*

The 2 adult pairs were on the same host, one pair in each gill chamber. The females have very broad frontal plates and the pleopods have relatively elongate endopods (Fig. 5a, b). One female agrees otherwise with the specimens from *U. pugilator*, especially in the gibbous digitations of the pleopodal exopods. The other female (Fig. 5c) differs in that the dorsal surface of the thorax is not raised into a longitudinal carina, and it has no dorsal bosses. The males (Fig. 5d, e) are identical with those of the parasites from the other species of *Uca* except for the greater length of the uropods.

Leidya bimini Pearse

Figures 6a-c

Leidya Rathbun, 1918, p. 248.

Leidya distorta (Leidy).—Richardson, 1908, pp. 22–26, fig. 1–5.—Verrill, 1908, p. 323 [Footnote].

Leidya bimini Pearse, 1951, p. 368–369, fig. 77a-i.—Hartnoll, 1965, p. 135.

Material examined: From *Pachygrapsus transversus* (Gibbes): 4♀♀, 1♂, Bermuda, 1901, A. E. Verrill, coll. (USNM 39246).—1♀, Bimini, Bahamas, 16 October 1948, A. S. Pearse, coll. (USNM 88598).—1♀, 1♂, Jamaica, R. Hartnoll, coll. (USNM 111346).—6♀♀, 4♂♂, Molasses Key, Florida, December 1968, R. Heard, coll. (USNM 128469).

Female:

a. Preadult.

Length 4.9 mm. The only specimen of this stage resembles closely, in dorsal view, the female of *L. distorta* shown in Fig. 1c, but the pleopods have distinct differences. The exopod of pleopod 1 does not reach beyond the epimeral plate; there is no blunt lobe between the exopod and endopod, and the endopods are very rudimentary.

b. Adult (Fig. 6a).

Length up to 6.6 mm. Cephalic plates, maxillipeds, pleural bosses, oostegites, and pereopods similar to those of *L. distorta*. Dorsal bosses, on pereonites 2–5, differ distinctly in being more or less bilobed posteriorly, especially pereonite 5 boss, which is deeply divided. Pereonites 6 divided in middle by longitudinal fissure. Pereopods relatively smaller. Biramous condition of pleopods (Fig. 6b) difficult to discern because of rudimentary condition of endopods: endopods of one side resemble exopods, but are much smaller; endopods of other side represented, at least in anterior pleonites, by small, slightly digitate processes which may be confused with base of exopod, to which they are closely attached. Epimeral plates about as long as exopods.

Variation:

—Cephalic plates (Fig. 6c) denticulate in several specimens.

—Dorsal bosses may vary in number from 2 to 4. Posteriormost boss always on pereonite 5, usually at midline, but in one specimen they are aligned diagonally from the pleural boss of pereonite 2.

Male:

Differs from *L. distorta* only in that medioventral tubercles are more strongly developed and are present on pleonites 1–5.

Conclusions

1. As stated in the introduction, the inadequate diagnoses, the doubtful value of the specific criteria used, and the different conclusions ar-

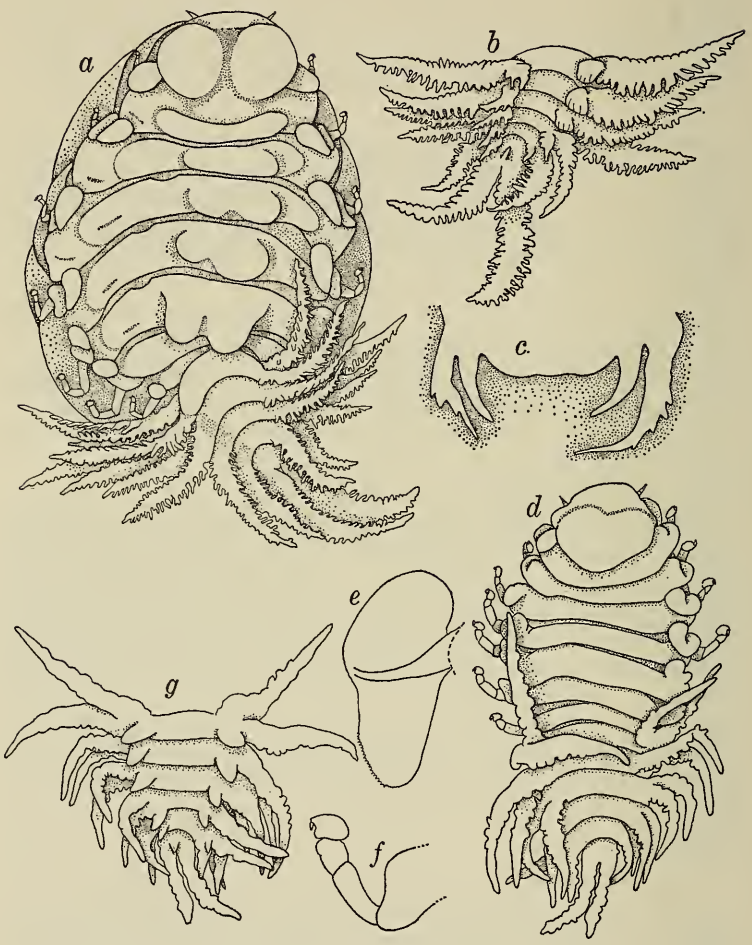

FIG. 6. a-c *Leidya bimini*, from *Pachygrapsus transversus*, adult female; a, habitus, dorsal; b, pleon, ventral; c, cephalic plates; d-g, bopyrid from *Cyclograpsus integer*, preadult female; d, habitus, dorsal; e, 1st oostegite; f, pereopod; g, pleon, ventral.

rived at by Richardson (1908) and Pearse (1951) made a reexamination of the parasites of *Uca pugilator* and *Pachygrapsus transversus* desirable. The study of the present material, which includes specimens used by Richardson and Pearse, has enabled us to confirm the heretofore uncertain validity and distinctness of *Leidya distorta* and *L. bimini*. As noted before, the only seemingly valid difference between the 2 species that can be derived from a comparison of previously published descriptions is the presence of medioventral tubercles in the male *L. bimini* and their apparent absence from *L. distorta*, since Leidy did not mention them. But, as we have indicated, males of both species have these tubercles on all pereonites; in *L. bimini* they are also present on pleonites 1–5, but in *L. distorta* they are limited to pleonites 1–2.

2. Our observations thus diminish the difference between the males of the 2 species, but fortunately the adult females may be easily distinguished by a number of characters, especially the following:

Character	*L. distorta*	*L. bimini*
Dorsal thoracic bosses	All simple, most often displaced to one side.	Posterior bosses bifid usually in middle of posterior margin
Exopods of pleopods of convex side	Much longer than epimeral plates, with blunt lobe at base.	Slightly longer than epimeral plates, without blunt lobe at base.
Endopod of pleopods	Relatively well developed and easily visible.	Rudimentary and difficult to distinguish.

Altho they differ slightly from corresponding stages taken from *Uca pugilator*, the young females found on *Uca* spp., *U. minax*, and *U. pugnax* all appear to belong to the same species, *Leidya distorta*. Differences in size, body form, more or less precocious development of the pleural bosses and the digitations of the pleopods can probably be attributed to an imperfect synchronization of the development of these characters with that of the marsupium, as is known to occur in *Cancricepon elegans* Giard and Bonnier (Bourdon, 1968).

3. Concerning the specimens from *Uca vocator*, the first is unquestionably *L. distorta*, in spite of the broad frontal plate. The second is referred to *L. distorta* with some reservations, for it is the only mature individual completely lacking dorsal thoracic bosses. The limited number of specimens of *Leidya* available makes it impossible for us to decide whether the absence of bosses represents an extreme degree of intraspecific variation or is a character of a distinct species of *Leidya*. The latter possibility cannot be rejected offhand; the presence of 2 parasites

on the same host does not prove that they belong to the same species, since instances of simultaneous infestation of a decapod by more than one species of bopyrid are known.

4. It is not possible to confirm that the parasite of *Cyclograpsus integer* (Fig. 6d-g), identified as *Leidya bimini* by the junior author (Hartnoll, 1965), actually belongs to this species. The 1st oostegite and the pereopods certainly agree with those of Hartnoll's bopyrid from *Pachygrapsus transversus*, but other characters show too many differences. Altho the specimen is already preadult its length is only 2.8 mm; the endopods of the pleopods are very distinct; the appendages of the pleon are coarsely tuberculate; the 5th oostegites are nearly as large as the 4th and have neither surface granules nor marginal setae.

5. Perhaps the most interesting result of the observations reported herein is that, contrary to previous descriptions, the females of both species of *Leidya* possess pleopodal endopods, and especially, that mediodorsal bosses are sometimes absent in this genus.

The significance of the latter variation is evident in view of the fact that the classification of the *Cepon* group of bopyrid genera is based upon the presence or absence of these bosses. Fortunately *Leidya* can be distinguished easily and with certainty from other crab parasites by the long filiform uropods of the male.

6. Two monospecific genera, *Megacepon* George and *Cardiocepon* Nobili, show particular affinities to *Leidya* that should be emphasized. The female of *Megacepon* differs from *Leidya* in having a large triangular dorsal boss on pereonite 7 (George, 1947; Shiino, 1958), and the female of *Cardiocepon* differs in that its pleon has biramous epimeral plates (Nobili, 1906). Otherwise both of these Indo-Pacific forms resemble certain specimens of *Leidya distorta* in their general habitus, the reduced frontal lamina, and the development and fimbriation of the pleon. The elongation of the posterior lamella of the 1st oostegite, unusual in the *Cepon*-group, is another important character shared by the 3 genera. Moreover all 3 genera infest catometopous crabs belonging to the families Gecarcinidae and Grapsidae. Both *Leidya sesarmae* Pearse (1930, known only from a single male, and *Megacepon choprae* George (1947), known only from the female, infest the same host, *Sesarma dehaani* H. Milne-Edwards, and it is quite possible that they are conspecific. The question of the identity of *Cardiocepon* and *Megacepon* with *Leidya* cannot be resolved until the characters of the males of the first 2 genera become fully known.

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